A BRIEF ANALYSIS OF VIVIPARITY IN INSECTS

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Viviparity may be defined as the birth of offspring without an enveloping egg shell. By way of contrast, oviparity means the extrusion of eggs or offspring that are surrounded at birth with such a membrane. To speak of the first case as the deposition of living young and to say that eggs are laid in the second are frequently misleading and erroneous statements which appear in the literature. Birth products are usually living offspring in more or less advanced stages of development. Only deposited eggs that require subsequent fertilization contain no living offspring.

Every known variation in the production of the next generation may be found. There are parthenogenetic eggs requiring no male contribution, inseminated eggs in which the culminating act of fertilization is still to ensue after deposition, and extruded, fertilized eggs in the zygotic stage. Eggs are also laid that may contain embryos of any developmental age, even eggs with fully grown embryos ready to fend for themselves immediately upon extrusion and, finally, insects give birth to living offspring which have hatched from the egg within the mother's body, or the eggs may never have been initially provided with a shell. All these may be cited as examples of reproductive processes in insects. It is with the last phenomenon that we are now concerned, and even viviparous reproduction shows several variations in its expression.

A few years ago, the writer undertook a study of the reported methods of viviparous reproduction in the hope of discovering some underlying factor, or factors, common to all of them. The study revealed, first, that a surprisingly large number of orders possess at least some viviparous species; second, despite profound differences in viviparous reproduction, each species conforms to one of four general patterns, or types, in the reproductive process; third, the taxonomic relationship between orders gives no clue to the viviparous reproductive pattern followed by their species; fourth, related families within an order may possess species differing from one another as greatly as may the orders with respect to their viviparous patterns. From these facts we can, perhaps, conclude that viviparity has arisen independently several times without regard to the length of the evolutionary history of the species concerned.

It should at once be evident that viviparity makes necessary special cooperative adjustments on the part of both mother and offspring beyond the comparatively simple demands of oviparity. The viviparous types and some of the modifications required of parent and offspring may now be reviewed.

1. Ovoviviparity is that type in which the egg contains sufficient yolk to nourish the embryo till hatching occurs and the offspring is deposited. This is by far the most commonly encountered kind of viviparity, occurring, or said to occur, in Thysanoptera, Blattodea, Anoplura, Plectoptera, Homoptera, Lepidoptera, Coleoptera, Hymenoptera and many Diptera, especially in the families Sarcophagidæ, Tachinidæ and Anthomyidæ.

In ovoviviparity the maternal uterus is often greatly enlarged in saccular form or as an elongate, spirally-twisted, wide tube. The chorion, or egg-shell, is frequently reduced to a thin, delicate, elastic membrane. Maternal physiological processes are altered to limit ovulation to a single egg or a few eggs at a time over a prolonged reproductive life. Her nervous system is adjusted for the retention of eggs till hatching is accomplished rather than to deposit them at once after the manner of oviparous species.

The offspring that hatches from the egg must escape from the shell in the maternal uterus. This process is quite different from rupturing the dry and brittle chorion of a deposited egg with an abundance of room. The larva also must have undergone physiological changes, too, for it does not attack the maternal tissues but, upon deposition, will readily and immediately feed on the tissues of its host if it happens to belong to a predatory or parasitic species.

2. Adenotrophic viviparity includes those insects whose retained eggs contain sufficient yolk to nourish the embryo till hatching occurs. After hatching, special maternal organs nour-

ish the offspring throughout larval life. All the pupipara (Hippoboscidæ, Nycteribidæ, Streblidæ) and all species of the family Glossinidæ are of this type.

Females having this type of viviparity are physically and physiologically limited to very few ovulations, perhaps ten or fifteen, during their reproductive life. Further, the ovaries alternate in the production of eggs so only one offspring at a time is cared for by the mother. Accessory glands are altered to function as nutrient organs, from which the larva derives its sustenance till ready to pupate. The larva has lost most of its ability to move, retaining only sufficient musculature to carry on respiratory functions and, in the Glossinidæ, to burrow in the soil far enough to hide during the pupal stage.

3. Metagonadic viviparity is distinguished by the haemocoelous development of the offspring for the ovaries do not discharge the ova into genital ducts. Embryonic nutriment is derived from maternal tissues by absorption through a trophamnion or a trophserosa. The developed larva often devours practically all of the mother's internal anatomy. Examples of this type of viviparity occur in certain Diptera (*Miastor,* etc.) and all species of Strepsiptera.

Diptera with metagonadic viviparity exhibit parthenogenesis in their viviparous phase although functional males appear seasonally and the species then becomes oviparous for a generation. The embryo absorbs nutriment from the surrounding maternal tissues. The larva becomes a parasite and, contrary to the larva of ovoviviparous species, immediately acts as a predator within its mother. It devours her internal organs and must eventually cut its own opening in the mother's body wall in order to escape. Strepsipterous females never develop into the adult form typical of most insects but remain larva-like in appearance. The reproductive organs have disappeared except for the ovaries which cast their ova into the hæmocœlar space where they lodge in the vicinity of the lobes of the fat body. This tissue is absorbed by the embryo. When the larva is ready to emerge from the maternal body cavity it does so, not by way of reproductive ducts, but through minute canals segmentally distributed along the maternal abdomen.

4. Pseudoplacental viviparity includes insects whose embryos within the genital tract obtain at least part of their nutriment by means of a pseudoplacenta. In every instance of this type of viviparity one notes that the offspring has succeeded in adapting itself to uterine life by the utilization of accessory, extra-embryonic structures normally quite passive, so far as has been ascertained in oviparous species, or it has recalled to active service degenerating organs, thought to be no longer of critical importance, and has given them new functions never before assigned to them. In the first case, the serosa or the amnion, or both, have taken over the rôle of nutrition while in the second, the much-discussed first abdominal appendages (pleuropodia) have assumed this function. It is the sole type of reproduction in which the embryo is more than a passive recipient of embryonic nutrition. Insects possessing this type of viviparity are some Dermaptera, Blattodea, Anoplura, Hemiptera and all Aphididæ.

The maternal and larval adjustments to the viviparous condition more nearly approach those recited for the ovoviviparous type. The offspring are deposited at the same developmental age in both types, corresponding to the freshly hatched embryo of an oviparously produced insect. There is no retention in the maternal body of later larval stages nor their oral nutrition as was the case in adenotrophic and metagonadic types of viviparity.

From this review of the types of viviparity, we may now draw a second conclusion, that is: the viviparous condition has developed in several instances to its present manifestations by different evolutionary processes in closely related species. As two examples to illustrate the meaning of this conclusion it is sufficient to recall that polyembryony appears in some Strepsiptera while the majority lack this interpolation in their metagonadic reproduction. More conclusively, the Diptera have representative species in three of the four types of viviparity.

As in the preceding discussion, we must content ourselves now with a very brief consideration of the evolutionary significance of the viviparous condition. Ovoviviparity may be considered the most elementary type of viviparity and the one most easily achieved. This type digresses least from the oviparous condition and, indeed, some insects show it only infrequently and usually are not viviparous in most of their reproductive activity. Others, such as the examples furnished, are constantly ovoviviparous but show relatively minor adjustments to viviparity in contrast to the three remaining types. However, these three types can, conceivably, be derived from ovoviviparity and it is possible they have thus arisen. In the adenotrophic type, for example, evolutionary progression has resulted, perhaps, from changes foreshadowed by a few extreme cases in ovoviviparity (*Mesembrina meridiana*, *Musca larvipara*). Pseudoplacental viviparity, too, may merely employ in a different way structures commonly present in ovoviviparous species, while the gradual loss of the reproductive ducts in the metagonadic type could be considered a reduction of the parts originally present before evolution removed them.

These statements would lead one to assume that oviparity preceded viviparity: this seems to be a sound conclusion. There is, certainly, much evidence in favor of this position with none to prove the reverse might be true. It is an evolutionary axiom that lost parts are not regained. If viviparity arose from oviparity then several absent parts in various viviparous species, (seminal receptacles, chorion of the egg, oviducts and yolk) can be explained away as evolutionary losses. It would certainly be more difficult to account for their uniform appearance in oviparous species as new developments from viviparous ancestors, especially for those who also believe in the polyphyletic origin of insects.

Finally, it would appear from a careful examination of the maternal structures affected in the known ovoviviparous insects, and in those that are occasionally ovoviviparous under certain conditions, that viviparity is a potentially important reproductive process, destined to supplant oviparity in a vast number of species. It entails some additional hardships on the mother but is, in the long run, the more economical process of perpetuating the species. With few exceptions viviparous species are numerous, specialized and highly successful in survival values. A population is maintained, not alone by the reproductive rate but equally by its death rate. Viviparous insects possess a very restricted biotic potential compared with related oviparous species but maternal care and protection, the lessened drain of yolk production in bearing limited numbers of offspring, and the reduced death rate of these offspring are essential savings that make it appear that viviparity is a decidedly favorable survival factor in hexapod life.